INTERNATIONAL *ARCHAEOPTERYX* CONFERENCE

The International *Archaeopteryx* Conference, sponsored by the Jura Museum, was held at Eichstätt, Bavaria, September 11 to 15, 1984, where most of the world's scholars of the earliest bird gathered. It had been hoped that all five *Archaeopteryx* skeletal specimens would be present, but this was not possible. Present were the Eichstätt specimen, the jewel of the Jura Museum collections; the very incomplete Haarlem specimen; and the magnificent Munich specimen of *Compsognathus*, the coelurosaur that compares closely with *Archaeopteryx*, its contemporary. The 66 registrants listened to 34 wide-ranging presentations. In addition, two field trips were made to quarries of the Solnhofen Limestone from which all specimens of *Archaeopteryx* have come.

Many quarries, situated in a zone from 15 km west of Eichstätt to 35 km east, remain active today, and slabs of the lithographic limestone are still hand-split in the time-honored manner. Sedimentary environments, elucidated by G. Viohl (Eichstätt) and P. H. de Buisonjé (Amsterdam), may impose some constraints upon interpretations of *Archaeopteryx*. The climate in the Upper Jurassic Tithonian at 30° north latitude was hot and arid, too dry to support trees. The lithographic limestone was deposited in a deep (to 200 m) back-reef lagoon, with a lifeless anoxic bottom. The lagoon was bounded by dead algal-sponge reefs, some of which may have been small islands. The Central German landmass to the northwest may have been the home of *Archaeopteryx*, or it may have lived on the small reef islands, and flew between them. Fossils in the limestone include diverse terrestrial insects and shrub-like conifers, as well as marine vertebrates and invertebrates (but almost no benthonic organisms).

A. J. Charig (London) led off the presentations with the sensible warning that the origin of *Archaeopteryx* is not necessarily the same as the origin of birds, and that the origin of birds is not necessarily the same as the origin of flight. These were sometimes forgotten. The major questions discussed dealt with the origins of *Archaeopteryx* (thecodont, crocodile, or theropod dinosaur), the relationship of *Archaeopteryx* to living and fossil birds (the first bird or a feathered reptile), the arboreal or terrestrial nature of *Archaeopteryx*, and the analysis of the origin of flight (from the ground up or from the trees down).

J. H. Ostrom (Yale) elegantly restated his position on the theropod ancestry of *Archaeopteryx*, and countered previously-raised criticisms of Tarsitano and Hecht concerning interpretation and significance of the fusion of the metatarsals, the reflexed hallux, and the structure of the coracoid, the pubis, and the lunate carpal in theropods, *Archaeopteryx*, and birds. J. Gauthier (Ann Arbor, Michigan) offered a detailed cladistic analysis of archosaurs that reinforced the notion of relationship between coelurosaurs and birds. Tarsitano and Hecht had previously argued for thecodont ancestry of *Archaeopteryx*, and Walker and Martin had each independently inferred crocodilian ancestry, but none chose to argue his preferred group. By default, theropod ancestry represented the consensus. An extreme variant was offered by G. Paul (Baltimore), who suggested in his abstract that the Upper Cretaceous theropods *Dromaeosaurus* and *Saurornithoides* were ground-living descendants of *Archaeopteryx*! He was unable to be present to defend this interesting proposition.

So strong seems the case for theropod ancestry that it might be proposed that *Archaeopteryx* was a coelurosaur that had nothing to do with birds. This proposition was unanimously rejected. A. Feduccia (Chapel Hill, North Carolina) argued eloquently that the avian feather is a unique, highly complex organ that could not have appeared more than once, and that the feathers of *Archaeopteryx* were avian in every detail. L. D. Martin (Lawrence, Kansas) reasoned that *Archaeopteryx* was a bird, but one that differed from modern birds in some important details, for instance in lacking a tarsal cap on the fused metatarsus. It shares a number of features with later Mesozoic birds, which thus represent an early sidebranch of avian evolution. A. D. Walker (Newcastle upon Tyne) presented an elegant and lucid analysis of the morphology of the ear region of *Archaeopteryx* and showed that, contrary to previous assessments, this region is very similar to the otic region of modern birds; in fact, it appears to be more like that of carinates rather than ratites.

Embryologist J. R. Hinchliffe (Aberystwth, Wales) advanced the most significant challenge to an otherwise tidy story in which *Archaeopteryx* is seen an annectant between coelurosaurs and birds. He claims to have confirmed, using modern isotopic techniques on chick embryos, that the hand of birds consists of digits II, III, and IV. He also reports a zone of mesenchymal cell death along the cranial edge of the wing, which further supports the idea of loss of digit I in modern birds. If this is true, it could mean that paleontologists have incorrectly interpreted the pattern of digital reduction in theropods (held to involve loss of digits IV and V), but this seems unlikely. It could also mean that, as a good theropod, *Archaeopteryx* had nothing to do with birds, which is also unlikely. Paleontological skepticism towards Hinchliffe's interpretation centers on the fact that no bird embryo is known to possess five digits; only such an embryo could incontrovertibly resolve the problem of digital reduction, but for the time being it remains a significant impasse.

In the 1970s, Ostrom argued effectively in a series of papers that *Archaeopteryx* was morphologically similar to undoubtedly terrestrial coelurosaurs, particularly *Compsognathus*. Moreover, its unguals were comparable to those of ground birds such as fowl rather than to those of perching birds. In a truly stunning paper, D. W. Yalden (Manchester) demonstrated that the unguals of the manus are nearly identical in morphology to those of tree climbers (*e.g.*, bats, dermopterans, squirrels) and contrast with those of predators. He reached this surprising conclusion by studying unguals in dorsal aspect, rather than in lateral aspect as Ostrom had done. Climbers have unguals that are long, thin, and parellel-sided, with a thick dorsal rib for strength--which describes the manus unguals of *Archaeopterx* to a "T". By contrast, the unguals of predators are broad at the base and taper steadily towards the apex. Ostrom was the first to stand up and congratulate Yalden, and was a model of grace in accepting the rebuff of one of his cherished ideas. Ostrom and others argued that *Archaeopteryx* was in all probability broad in its habits, making use of both ground and trees in its normal range of activities. Feduccia evoked the lesson of the basilisk, which runs on land and across water, climbs trees, swims in the water, and walks on the bottom of lakes--none of which activities are evident from its morphology.

Prior to Ostrom's studies, most authors had sought the origin of flight in the trees. Ostrom, however, in his analysis of *Archaeopteryx* as a terrestrial cursor, argued forcefully for the origin of flight from the ground up. In 1983, this position received a considerable boost with the publication by G. Caple, R. P. Balda, and W. R. Willis (Flagstaff) of an analysis of the energetics of leaping and flapping. They concluded that the scenario of flight originating from the ground up is energetically possible and plausible. At this conference they restated their position. Speaking for the trio, Balda argued against gliding as a precursor to powered flight, a position also championed recently by Padian. They argued that parachuting would result in fatal crashes, that flapping during stable glides would be more likely to create stalling than to generate lift, and that bipedal landing in trees in the absence of sophisticated control of powered flight is hazardous.

The arguments of the Flagstaff group paled before a brilliant presentation by J. M. V. Rayner (Bristol), a self-professed experimental biologist and mathematician. Rayner's strengths were three-fold: a feeling for living powered flyers, especially bats and birds; a sophisticated understanding of the dynamics of flapping flight, a subject that has long daunted aerodynamic engineers; and a fine ability to carry an audience along with him rather than to overwhelm them. He argued that gliding is an excellent precursor for flapping flight, and that gliding is a superb energy-conserving method of "commuting" across a forest. Selection would naturally favor an increase in gliding range, and that an aspect ratio (ratio of length of a wing to its width) as low as three (*i.e.*, *Archaeopteryx*) is adequate for horizontal flight. The function of flapping is to provide not lift but forward thrust. The Rayner model envisages a smooth transition from gliding to slow flapping to improved flapping with the development of the supracoracoideus wing elevation system. U. M. Norberg (Göteborg, Sweden) followed with another detailed aerodynamic analysis of flapping, and also concluded that even limited flapping would increase the length of a glide. Selection for increased wing length would have decreased gliding speed, leading to safer landings.

With a flair for the dramatic and an instinct for the coup de grace, Rayner announced his intention to perform calculations in his room that night on the energetics of the Flagstaff model for the transition from running to flying. The next day he reported that it could work if certain conditions were met: namely that a cursor could run at 10 m per second, could launch itself upward at an angle of 10°, and could glide upward one-quarter of a meter. It would then have the time for three wing strokes; if there were vertical space sufficient for three wing strokes symmetrical above and below the horizontal, it may be possible to achieve powered flight. He left little doubt that these were improbable conditions for a protoflyer. Effectively the concept of flight from the ground up was left in shreds, and no effective support for this idea was heard for the rest of the conference. Combined with Yalden's evidence, there seemed little doubt among the majority of participants that *Archaeopteryx* had been returned to the trees.

In a truly original presentation, R. A. Thulborn (Queensland, Australia) argued from a literal reading of the fossil record that *Archaeopteryx* was an inhabitant of the seashore, wading in the shallows to capture worms, crustaceans, and small fishes, and using its wings as a canopy to reduce glare and improve visibility. He failed to convince. M. E. Howgate (London) argued from the small size of the Eichstätt specimen (about two-thirds the linear size of the other specimens), combined with its high degree of ossification, absence of furcula, orientation of the pubis, and differences in dentition from the Berlin specimen, that the Eichstätt specimen represents a distinct genus of bird. Discussants pointed out that if a reptilian mode of indeterminate growth prevailed, his arguments would lose much of their force, and that ontogenetic changes of tooth shape are well known among modern lizards. Howgate's proposal, too, failed to convince.

At the end of the three days of presentations, Charig orchestrated a concerted effort to summarize the ideas for which a general consensus exists. The general credo runs like this. *Archaeopteryx* was a bird that could fly, but it was not the direct ancestor of modern birds. It was a bipedal cursor that was facultatively arboreal. Flight developed with the assist of gravity (*e.g.*, from the trees down) rather than against gravity (from the ground up). *Archaeopteryx* was probably derived from theropods. A communique expressing the unanimous belief of all participants in the evolutionary origin and significance of *Archaeopteryx* was adopted in order to forestall the malicious misuse by creationists of apparent discord among scientists. Problems identified for discussion at a future conference include the identification of the digits of modern birds; the anatomy of the pelvis, the ear region, the lower jaw, and the shoulder; the formulation of alternative phylogenies for bird ancestors; and an examination of thecodonts. The conference was exciting and productive, and its success is greatly to the credit of Dr. Gunter Viohl and the Jura Museum, and to Dr. John Ostrom.

Copies of the proceedings may be ordered from Dr. John H. Ostrom, Peabody Museum of Natural History, Yale University, P.O. Box 6666, New Haven, Connecticut 06511, before March 1, 1985. The U.S. price is $24.00; the German price (ordered from the Jura Museum, 8078 Eichstätt) is DM 70.00. Expected publication date is mid-1985.

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2. Articles must be of interest both to amateur and professional members of the paleontological community

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